TRANS-OCEANIC POPULATION GENETIC STRUCTURE OF HUMPBACK WHALES IN THE NORTH AND SOUTH PACIFIC

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We examined genetic diversity of humpback whales in the North and adjacent South Pacific Oceans to investigate the history and dynamics that resulted in their current population structure and for which trans-oceanic gene flow is a phenomenon of great importance. Analysis of mitochondrial DNA variation suggests that humpback whale populations are subjected to contraction and expansion cycles associated with glaciations. Contrast between nuclear and mitochondrial genetic diversities show that expansion phases may be related to regional differentiation dependent upon sex-biased dispersal. To explain trans-oceanic gene flow from sex-biased dispersal, we analysed the species' wintering habits in the Mexican Pacific as described from the sex composition and temporal profile of social groupings. In consideration of the energetic burden for reproduction of female humpback whales and the resultant pre-copulatory competition among males, trans-oceanic gene flow may be explained by changes in winter distribution driven by male dispersal dynamics and gametic exchange across high productivity areas close to the equatorial coast of the American Pacific, as well as by the influence of long-term climatic change in forming trans-equatorial corridors for female interchange. Because of the sensitivity of humpback whale reproduction and dispersal to environment perturbations, our results raise concerns about the effects of climate change on the phylogeographic structure and thereby the evolution and long-term conservation of this species. ☐ *Humpback whale, gene flow, climate change, genetics.*

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In winter, humpback whales, *Megaptera novaeangliae*, return from high latitude summer feeding grounds to warm ca.25°C shallow waters in low latitudes (Dawbin, 1966). Although not well understood, the basis for this preference seems related to breeding, giving birth in an environment suitable to the thermoregulatory capabilities of newborns and for protection of calves from predators (Brodie, 1977; Lockyer & Brown, 1981). Because of the apparent dependence on water temperature in winter, the breeding ecology of humpback whales may be affected by climatic change. The Pacific coast of the Americas offers a unique biogeography for the study of this process and its influence on population history and structure.

The American Pacific coast bounds, from subpolar latitudes to the equator, the cool and highly productive streams of California and Humboldt which enhance primary productivity

around the equator by upwelling. In relation to coastline topography, the Humboldt Current extends north of the equator while the California Current swings westwards at Baja California Peninsula (Wyrtki, 1967; Love, 1975). As a result, humpback whale wintering grounds from Northern and Southern Hemispheres overlap in Central America (Acevedo & Smultca, 1995; Flórez-González et al., 1998; Calambokidis et al., 2000). Pacific Ocean born El Niño and La Niña oscillations provide a source of environmental variation that allows examination of changes in the ecology of migration that have driven the population history of North and South Pacific humpback whales as inferred from genetic analyses.

Elsewhere (Medrano-González et al., 1995; Baker & Medrano-González, in press), we have hypothesised that humpback whale populations are subjected to contraction/expansion cycles associated with glaciations. Apparently, on the American Pacific coast, during glacial times humpback whale populations may have been reduced by restricted feeding areas, a result of an extended ice front forcing distribution closer to the equator. Together with a reduced area of warm waters around the equator, this may have facilitated exchanges between Southern and Northern Hemisphere populations. During deglaciations, the feeding areas of humpback whales increased as the ice fronts retreated and the growing populations dispersed into new breeding areas for which the combination of phylopatry and dispersal generated the hierarchical phylogeographic structure observed today. This phenomenon may account for the recent origins of the Hawaiian stock at the end of the Little Ice Age as the coastlines of southeast and central Alaska opened for humpback whale feeding during the 18th and 19th Centuries (Herman, 1979). The Atlantic Ocean had a particular distribution of oceanographic conditions during glaciations with the North Atlantic being very cold with warmer temperatures of ~25°C in the Caribbean Sea (Ruddiman, 1987; COHMAP members, 1988; Williams et al., 1993). Thereby, the pattern of mitochondrial (mt) DNA diversity suggests that the current North Atlantic population of humpback whales has been largely introgressed by the Southern Ocean population through the Caribbean Sea. A study of nuclear genetic variation may provide further evidence to evaluate the extent and timing of the proposed recolonisation of humpback whales in the North Atlantic Ocean (Congdon et al., 2000; Baker & Medrano-González, in press).

The population history and structure of humpback whales is not solely a story in itself but also an enquiry into the interaction between the physical and biological factors that shape the phylogeographic structure and evolution of the species. Here we study the trans-oceanic population genetic structure of humpback whales looking for a set of interactions between different phenomenological levels that may be useful to understand the process of genetic differentiation in general. Such a search is possible by examining the history and mechanisms of trans-oceanic gene flow between the winter of one hemisphere and the winter of the other. Thus, to understand trans-oceanic migration, we should rely on the wintering habits, especially in terms of dispersal and changes in distribution. Here we concentrate on the Pacific coast of the Americas which has two humpback whale populations exhibiting gene flow between them and hierarchical differentiation within each (Medrano-González et al., 1995; Baker et al., 1998a,b; Baker & Medrano-González, in press). We review past publications, recent thesis works developed in México and unpublished data to describe the history and dynamics of gene flow along this coast. Comprehension of this phenomenon may provide insight into the future consequences of global climate change on the evolution of humpback and other baleen whales. Since we made a first approach to understand population history and phylogeographic structure from the habits and ecology of individuals, we invoked the dynamical systems theory which is briefly reviewed in the Appendix.

METHODS

GENETIC ANALYSIS. Skin samples of humpback whales were collected in waters of the Bransfield and De Gerlache Straits in Antarctica, the Colombian Pacific, the Mexican Pacific mainland coast, Socorro Island from the Revillagigedo Archipelago, the Southern coast of Baja California, the Californian coast, the Hawaiian Archipelago and the southeast Alaskan coast. Mitochondrial genetic diversity has been analysed by sequencing and determination of restriction fragment length polymophisms (RFLP) of a ~400BP segment from the mtDNA control region adjacent to the tPro gene. Nuclear variation was described by genotypes of four microsatellite loci: TAA 31, GATA 28, GATA 53 and GATA 417 (Palsbøll et al., 1997a). Data and techniques have been described by Baker et al. (1993, 1994, 1998a,b), Medrano-González (1993),

Medrano-González et al. (1995), Olavarría-Barrera (1999) and Baker & Medrano-González (in press). Original data still to be described are from Baker (unpubl. nuclear genetic data from Colombia, California, Hawaii and southeast Alaska), Robles-Saavedra (unpubl. mtDNA and sex identification data from México) and Vázquez-Cuevas (unpubl. nuclear genetic data from México). We used these data in a preliminary examination of sex-biased dispersal at different levels of population structure in the American Pacific (Fig. 1). Genetic diversity was described by Nei's index h (1987: 177) and population differentiation was determined from Wright's F_{st} (1969) as calculated by the variance analysis of Excoffier et al. (1992). Gene flow (Nm), the number of interpopulation migrants per generation, was estimated by the following Wright's (1969) approximation:

$$Nm = \frac{1}{P}\left(\frac{1}{F_{st}} - 1\right)$$

(1)

where the ploidy factor P equals 2 for mtDNA and 4 for nuclear genetic markers.

To calculate population expansions and clade divergence dates, the distribution of mtDNA coancestry time was analysed from the sequence data compiled by Baker & Medrano-González (in press) considering a nucleotide substitution rate of 1% per million years (MY), a male/female ratio of 1:1 and a female generation time of t_g=10 years (Chittleborough, 1958, 1965; Clapham & Mayo, 1987a,b; Hoelzel et al., 1991; Baker et al., 1993; Clapham et al., 1993; Martin & Palumbi, 1993; Clapham, 1996) (Fig. 2). This approach assumes that the molecular clock is valid at populational divergence time scales and thereby that population history dates depend mostly on population fragmentation/bottlenecking events. MtDNA coancestry-time distributions (p_t) were fitted to the following equation (Avise et al., 1988; Rogers & Harpending, 1992):

$$p_t = \left(1 - \frac{1}{N_f}\right)^t$$

(2)

where N_f is the long term effective population size as number of females and t is time in generations. We also tested whether the analysed fragment of mtDNA was neutral using Tajima's D test (1989a,b). A simulation for the expansion of the private mitochondrial haplotype most abundant in the Mexican mainland Pacific coast (AE) was performed to estimate the divergence

time between this aggregation and that of the Revillagigedo Islands (Fig. 3). We also estimated the coancestry time of mtDNA lineages to describe the divergence among two haploid populations due to genetic drift, starting from F_{st}=0, with the following equation, adapted from Weir (1990: 167), at time t:

$$F_{st(t)} = 1 - \left(1 - \frac{1}{N_f}\right)^t$$

(3)

The software 'Arlequin' 1.1 (Schneider et al., 1997) was used for most genetic calculations. Curve fitting was made with the least-squares procedure available in 'Sigmaplot' 1.02. Simulations were performed using the software 'Deriva', developed by Medrano-González (1993) and available upon request.

WINTERING HABITS ANALYSIS. Bahía Banderas in the Mexican mainland Pacific coast and Socorro Island from the Revillagigedo Archipelago were visited for humpback whale research from January to April, 1999. Observations on Socorro Island in this year were carried out with the logistic support of Salvatore Cerchio from the University of Michigan. Wintering habits of humpback whales were described by the occurrence profiles of pod and activity classes. A consensus definition of such classes follows based on Tyack & Whitehead (1983), Baker & Herman (1984), Baker (1985), Mobley & Herman (1985), Glockner-Ferrari & Ferrari, (1990), Clapham et al. (1992), Medrano et al. (1994), Brown & Corkeron (1995) and Darling & Bérubé (2001). These are: 1) Solos – juvenile and adult animals of both sexes which mostly transit between conspecific groups; 2) Singers – adult males which stay in a definite area for many hours vocalising songs to attract receptive females and/or to order social status; 3) Adult and/or juvenile pairs – allied males or a male and a female associated around mating; animals generally in transit (pairs of females seem to be very infrequent and unstable pods); 4) Female with a newborn; 5) Female with a newborn and escort – the escort being an adult or juvenile male presumably awaiting the oestrus of the cow; 6) Groups – three or more adults or juveniles; a calf and cow may be present. Humpback whale groups have been described as groups of males in competition. There is normally a nuclear female around which males exhibit agonistic behaviour. Agonistic interactions in groups, however, may occur without a female present.

Sex composition of pods was determined using the method of Palsboll et al. (1992; Medrano et al., 1994; Robles-Saavedra, unpubl. data). Relative size was judged by eye to distinguish the following classes of sex/reproductive status (*sr*): 1) Newborns; 2) Juvenile or adult males; 3) Juvenile or adult non nursing females; and 4) Nursing females. Temporal profiles of humpback whales wintering in the Mexican Pacific were analysed weekly and relative abundance was determined from the number of sightings per hour of boat-based search and observation (Fig. 5). Abundance of each sex/reproductive status class (f_{sr}) was calculated combining the data of sex composition and occurrence of pods as follows:

$$f_{sr} = \sum_g f_g N_g Q_{srg}$$

(4)

where f_g is the abundance of pod g, N_g is the average size of g and Q_{srg} is the fraction of individuals of the class sr in g (Table 1). Encounter rate between males (m) and females (f, both nursing and non-nursing) was determined as the product of their respective abundances, i.e. f_m f_f. Encounter rate between males was calculated as f_m^2.

RESULTS AND DISCUSSION

GLOBAL LINEAGE DISTRIBUTION AND TRANS-OCEANIC GENE FLOW. Previous descriptions of the global structure of mtDNA variation in humpback whales demonstrate differentiation among and within the three oceanic populations: North Pacific, North Atlantic and Southern Ocean (Baker et al., 1993, 1994; Baker & Medrano-González, in press). Baker et al. (1993) described the grouping of world-wide mtDNA lineages into three clades, referred to as CD, IJ and AE, with categorical and frequency differences in the three oceans. The CD clade was found in each of the three oceans and was numerically dominant in the Southern Hemisphere. The IJ clade was most abundant in the North Atlantic, showing a clinal increase in frequency across feeding grounds from the Gulf of Maine to Norway (Palsboll et al., 1995; Larsen et al., 1996; Baker & Medrano-González, in press). The IJ clade was present in all regional populations examined to date in the Southern Hemisphere but entirely absent in the North Pacific. The AE clade was most abundant in the North Pacific showing a clinal increase, especially in the subtype A, from a very low

frequency on the California feeding grounds to fixation on the Alaskan feeding grounds. The AE clade was also found in low frequency on the Colombian wintering ground and the Antarctic feeding ground but is absent from other Southern Hemisphere regions and the North Atlantic Ocean (Baker et al., 1993, 1994, 1998a,b; Medrano-González et al., 1995; Baker & Medrano-González, in press).

Although this global distribution of humpback whale mtDNA lineages supports, in general, the assumption of isolation of oceanic populations by continental landmasses and the seasonal opposition of the hemispheres, it also suggests a corridor of gene flow or interchange along the Pacific coast of the Americas. The CD clade is found in high frequency on both Colombian and Mexican wintering grounds, indicating at least past migration from the Southern Ocean to the North Pacific. A smaller frequency of individuals with identical mtDNA haplotypes in both regions suggests more recent gene flow in this direction. Similarly, the low frequency of the AE clade in Colombian and Antarctic Peninsula region suggest a lower rate of historical exchange from the North Pacific to the south (Fig. 1).

For microsatellites, very similar patterns of molecular size distribution are observed in the Antarctic Peninsula and along the American Pacific coast. In general, nuclear genetic markers exhibit a smaller differentiation, as compared with mtDNA, within and between oceanic populations (Palumbi & Baker, 1994; Valsecchi et al., 1997; Baker et al., 1998b) suggesting that male gene flow is larger than that of females (Fig. 1). These patterns support the idea that nuclear genetic markers provide a historical perspective different from that of mtDNA (Congdon et al., 2000). Because variation of microsatellites consists basically on the number of oligonucleotide repeats, these genetic markers evolve with a high degree of homoplasy and their analysis is thus poorly informative for phylogenetic inferences. However, microsatellite mutations yielding imperfect repeats generate different repeat frames which may identify different allelic lineages and thus, dispersal events as well as mutation trends. In humpback whales from the American Pacific, for example, four repeat frames may be found in the locus GATA 28. Described with the molecular size of the PCR products based on the primers of Palsboll et al. (1997a), these frames are 147-155BP, 156-176BP, 154-190BP and 185-189BP. Given the geographic and molecular size distributions of each frame and assuming that

TABLE 1. Composition of sex and reproductive status classes (Q_{srg}) for different humpback whale pods in the Mexican Pacific. Males and non nursing females include juveniles and adults. Data from Medrano et al. (1994) and unpublished results of Robles-Saavedra. * 6 adults sampled, all females; ** 5 assumed escorts, males, and 9 assumed cows, females; *** N = number of animals in the pod.

Pod	Sample size	Newborns	Males	Non nursing females	Nursing females
Solo	11	-	0.73	0.27	-
Singer	3	-	1.00	-	-
Pair	32	-	0.78	0.22	-
Cow/calf*	6	0.50	-	-	0.50
Cow/calf/escort**	14	0.33	0.33	-	0.33
Group	55	-	0.87	0.13	-
Group/calf***	-	1/N	(N-2)/N	-	1/N

such frames are originated by 3BP imperfect repeats of the GATA 28 tetramer, we have built an hypotethical evolutionary pathway between the four repeat frames (Fig. 1). This pathway shows that the repeat frame lineage 185-189BP has originated from the alleles 182BP or 186BP recently in the east South Pacific and has not migrated to the east North Pacific. Thus, coalescent models using the frequency of the private alleles (see below) could give an estimate for the most recent separation between the North and South Pacific. For the locus GATA 53 the frames 195-199BP, 201-209BP and 202-210BP have been found in the Mexican Pacific only, providing an opportunity to estimate the divergence between these wintering aggregations and those of Hawaii (Fig. 1). The evolutionary pathways illustrated show that some microsatellite lineages have recently originated, as the frame 185-189BP of locus GATA 28, while others may be reminiscent, as the frame 156-176BP of locus GATA 28 which is rare, as well as widely but discontinuously distributed in both molecular size and geography. Since the apparently most recent frame lineages (those with short and continuous molecular size and geographic distributions) are longer than the apparently older frame lineages (Fig. 1), a general trend of increase in microsatellite size may be deduced from our analyses according to what is apparent also in other mammals (Rubinsztein et al., 1995). Cloning and sequencing of the different microsatellite alleles is necessary for a proper phylogenetic interpretation of the repeat frames and thus a comprehensive analysis of these topics need to be developed elsewhere.

RECENT AND HISTORICAL POPULATION CHANGES AND TRANS-OCEANIC GENE FLOW. For North and South Pacific humpback whales, and for separate CD and AE types,

Tajima's (1989a,b) neutrality test shows a deficiency of nucleotide differences between individuals as expected from the number of polymorphic sites in the examined fragment of mtDNA. This suggests that mtDNA variation of humpback whales in the North and South Pacific has been affected by a population reduction. In order to know whether this reduction of genetic diversity is related to exploitation by humans we may consider an exploitation worst-scenario for the species in the North Pacific with $N_f = 250$ following Rice (1974) and considering a male/female proportion of 1:1 during 10 generations (100 years). Following Wright's formulation (1931: 111; Nei, 1987: 360), genetic drift in these conditions is expected to have diminished mtDNA diversity to a proportion of $H_t/H_o = (1-(1/N_f))^t = 0.96$ from its original value (H_o). Consideration of the levels and geographic patterns of mtDNA variation world-wide also indicates that humpback whale genetic diversity has not been much affected by humans (Baker et al., 1993, 1994). Therefore, humpback whale mtDNA variation keeps information about historical fluctuations of gene flow, population fragmentation and abundance.

The mtDNA coancestry distribution of humpback whales world-wide shows two expansion waves, with mean times of ~230,000 and ~1,500,000 years, assuming a substitution rate of 1% per million years (MY), which correspond to intra and interclade variations respectively (Fig. 2). To analyse single expansions, we have then examined intraclade and intrapopulation variation fitting the mismatch distribution to equation (2) according to Avise et al. (1988). Average coancestry times in the North Pacific are 145,000 years for the AE clade and 130,000 years for the CD clade. Insufficient data exist to analyse the mismatch distribution of AE types in the
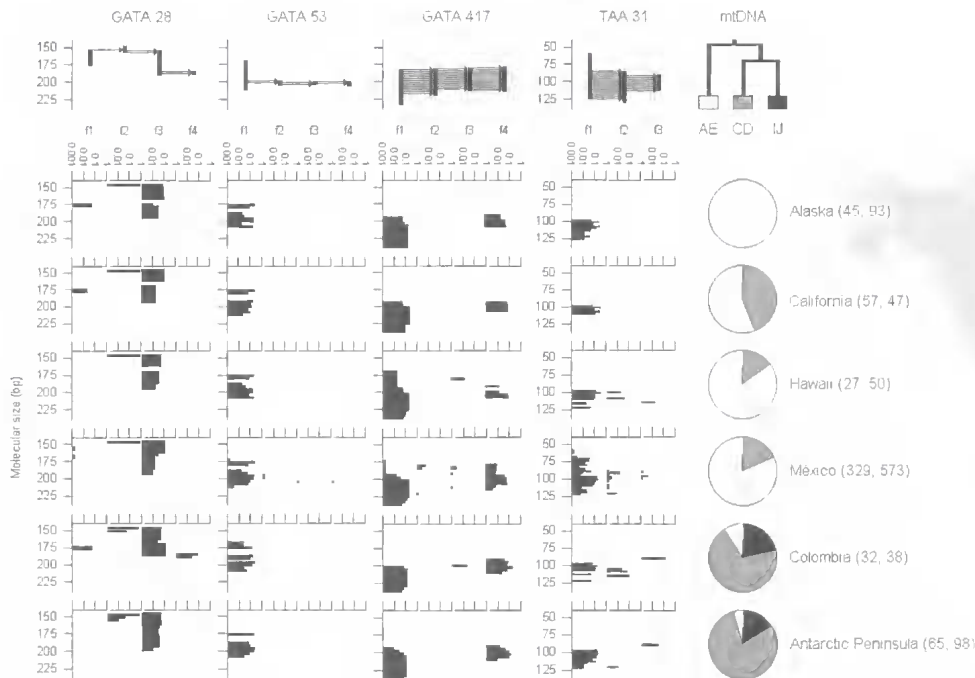
FIG. 1. Genetic variation of mtDNA control region and 4 microsatellite loci in humpback whales from the American Pacific coast and the Antarctic Peninsula. Parentheses indicate sample size as number of mitochondrial haplotypes and average number of microsatellite alleles per locus. Distribution of microsatellite molecular size in base pairs (bp) is plotted for the 3 or 4 sequence repeat frames (f1, f2, f3 and f4). Frequency scale for each frame is logarithmic from 0.001-1. Phylogeny of the three main mtDNA clades and evolutionary pathways between the different microsatellite repeat frames are sketched in the top indicating with arrows all possible mutations of 3BP imperfect repeats for the GATA tetramers and mutations of 2BP imperfect repeats for the TAA trimers. Polarity from f1 to f4 or f3 has been hypothesised on the basis of molecular size and geographic distribution. Repeat frame lineage intervals are, respectively for f1, f2, f3 and f4, 156-176BP, 147-155BP, 154-190BP and 185-189BP for GATA 28; 168-212BP, 195-199BP, 202-210BP and 201-209BP for GATA 53; 182-234BP, 181-221BP, 180-212BP and 179-215BP for GATA 417; 59-125BP, 88-130BP and 90-114BP for TAA 31. MtDNA data are from Baker & Medrano-González (in press), Olavarría-Barrera (1999) and unpubl. results of Robles-Saavedra. Nuclear genetic data are from Olavarría-Barrera (1999) and unpubl. results from Baker & Vázquez-Cuevas.

Southern Ocean but they have a coancestry mean time of 110,000 years. The CD clade in the Southern Ocean has a bumpy-bell shaped distribution with mean of 950,000. These distributions roughly correspond to long term effective population sizes of over 14,000 females in the North Pacific and over 90,000 females in the Southern Ocean which exceed the pristine population size estimates of Rice (1974) and Chapman (1974) (Fig. 2). Coalescence within the North Pacific of AE and CD clades dating back 110,000-145,000 years corresponds to the end of Illinoian glaciation (Lorius et al., 1985). Phylogenetic analysis of mtDNA variation indicates that multiple and reverse trans-oceanic gene flow events have occurred at least for CD types. This

suggests a minimum of two trans-oceanic intermingling periods related to the Illinoian and Wisconsinian glaciations (Baker & Medrano-González, in press).

WITHIN OCEAN DIFFERENTIATION: ORIGINS OF THE OFFSHORE REVILLAGIGEDO BREEDING GROUNDS. Humpback whales from Revillagigedo Islands and from the Mexican Pacific coast are separate subpopulations which, being genetically similar, have presumably diverged recently from each other (Medrano-González et al., 1995; Urbán et al., 2000). Nucleotide mtDNA divergence between Mexican coast and Revillagigedo grounds is 0.018% which suggests a divergence time of 9,000 years considering a substitution
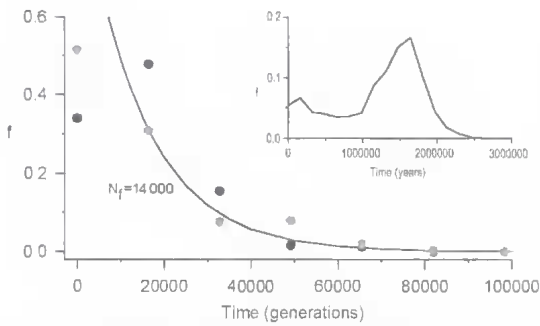
FIG. 2. Distribution of coancestry times for the mitochondrial AE (black, $n = 87$) and CD (gray, $n = 24$) clades in the North Pacific. The curve shows the function of equation (2) which fitted $N_f \sim 14000$ for both distributions. The inside graph shows the world-wide coancestry distribution ($n = 268$). Data from Baker & Medrano-González (in press).

rate of 1%/MY. This reasoning is constrained by the fact that genetic divergence is not due to a gene substitution event but to different haplotype frequencies and by the presence of private haplotypes, such as AE, E2, E3, E4 and F1, in the wintering grounds of the Mexican Pacific coast (Medrano-González et al., 1995). We considered that these types may serve for estimating the divergence time of Revillagigedo whales by looking for the time necessary for a newly arising mutant to reach current observed frequencies. We have simulated the propagation of a mito-chondrial and neutral mutant in hypothetic populations of humpback whales of size $N_f = 5,000$ to 15,000 females, generation time $t_g = 10$ years and reproductive rate $B_r = 0.1$ calves/individual, year. We used as reference the AE haplotype, a subtype of the AE clade, which has a frequency in coastal areas of $q = 0.05$ to 0.07 (Medrano-González et al. 1995; Robles-Saavedra, unpubl. data), since it is the most abundant among coastal private types. For different combinations of reference-q value and N_f, we made $2N_f$ simulations. In general, 400 to 900 generations take place for a mutant to reach the current frequency of the AE type (Fig. 3). Also, the current mtDNA differentiation between coastal and Revillagigedo humpback whales is $F_{st} = 0.11$ (Medrano-González et al., 1995) and the time to attain this value by genetic drift, starting from $F_{st} = 0$, was calculated with equation (3) and found to be 874 generations for $N_f = 7,500$ and 1,748 generations for $N_f = 15,000$. In summary, the nucleotide divergence of 0.018%, the origins of the AE haplotype in 400 to 900 generations ago and the attainment of current F_{st}

= 0.11, coincide to a divergence time between humpback whales from the Mexican Pacific coastal grounds and Revillagigedo Islands of 4,000-9,000 years ago which is the last deglaciation period (Lorius et al., 1985; COHMAP members, 1988).

MALE AND FEMALE GENE FLOW. The low nuclear genetic differentiation indicates that total gene flow among humpback whale populations is underestimated by equation (1) as it is valid only for small values of the per capita migration rate, m (Wright, 1969). Because of the much higher differentiation in mtDNA, it may be deduced that a large proportion of the humpback whale gene flow is owed to males (Palumbi & Baker, 1994; Baker et al., 1998b) (Fig. 4). However, for a direct comparison between total gene flow, determined from the population differentiation of nuclear loci and gene flow of females, determined from the differentiation of mtDNA, these genetic markers should have approximately equal mutation and fixation rates and thus, similar levels of diversity. In our data, the gene diversity index h, is in average for mtDNA 63% of the diversity found in microsatellites and this implies a relatively lower resolution of mtDNA to detect population structure. On the basis of genetic diversity then, mtDNA gene flow may be overestimated if contrasted with gene flow in nuclear loci. Therefore, the inaccurate estimation of total gene flow using equation (1) and the different molecular evolution rates of mtDNA and microsatellites seem irrelevant for a general view of sex-biased dispersal as the proportion of gene flow by males is apparently high and underestimated. Although, in principle, two sets of genetic variation data with different linkage to sex, nuclear and mitochondrial for example, should be enough to get independent estimates of male and female dispersal, the large proportion of males in nuclear gene flow fits their $1/f$-dispersal distribution at different population levels ad hoc to equation (1) since '~1 (Fig. 4; Appendix). An option to determine population differentiation and gene flow of males independently, is to analyse genetic variation in a haploid fragment of the Y chromosome. Our preliminary analytic expression for male dispersal in Fig. 4, suggests that male dispersal distributes as 'pink noise' and thus that it is associated to a chaotic dynamic process (Bak & Paczuski, 1995; Halley, 1996; Appendix). Female dispersal has no direct relationship with nuclear genetic differentiation. Because of their greater fidelity to migratory destinations, female dispersal should be more
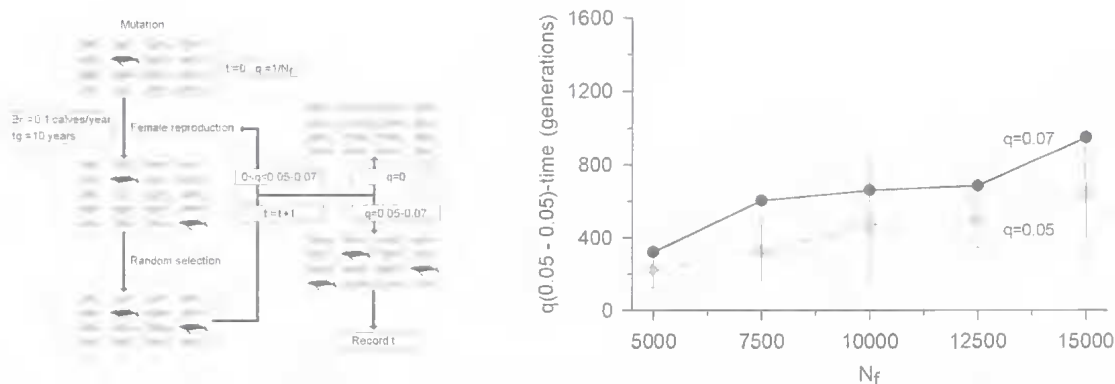
FIG. 3. Simulation of the AE haplotype expansion in the humpback whale aggregation of the Mexican Pacific coast. Left: Individual simulation flow chart starting with the appearance of a mutant (black whale) and showing changing values of time (t) and private haplotype frequency (q), fixed parameters of population size ($N_f = 5000$ to 15000), generation time ($t_g = 10$ years), birth rate ($B_r = 0.1$ calves/individual, year) and q reference value (0.05 or 0.07). Two points next to the equality in t or q mean that the value in the right side is assigned to the variable in the left. After any generation, the value of q may be zero (the simulation is then finished and a new one is started), over zero and under the reference value (the simulation goes to a new generation with its reproduction and selection cycle) or reach the reference value (the time as generations elapsed since the mutant apparition is recorded). Right: Simulated time to reach the reference values $q = 0.05$ or 0.07 for variable population size (N_f) performing $2N_f$ simulations in each case. Error bars represent standard deviation of 18 to 58 successful simulations.

subjected to historical contingencies such as a large intermingling between México and Colombia at least during the last two glaciations and an intra-oceanic divergence after the separation of a monophyletic founder group from which the Alaska/Hawaii stock derived at the end of the Little Ice Age (Fig. 4).

Sex biased dispersal of the humpback whale seems to derive from its polygynic mating system. Precopulatory competition among males makes them disperse into breeding areas seeking opportunities to mate while females are more phylopatric in relation to energetic burdens for reproduction (Brodie, 1977; Greenwood, 1980; Lockyer & Brown, 1981; Clapham, 1996). The difference in phylopatry between sexes is both spatial and temporal. Timing of migration between feeding and breeding areas, in which females stay for a short period in breeding areas or even winter along the migratory route without reaching breeding grounds, optimises the energy assimilation of females for reproduction and the chances of males to mate (Dawbin, 1966; Brown et al., 1995; Craig & Herman, 1997).

EXPANDING ICE, RETREATING WHALES. Our results suggest that glaciations have an homogenising effect on humpback whale populations because of habitat reduction and increased trans-oceanic genetic exchange while interglacial periods favour differentiation through reduced trans-oceanic gene flow and colonisation of regional habitats within oceans. This is contrary to many cases for which glaciations fragment populations in isolated refuges, for example belugas and narwhals (O'Corry-Crowe et al., 1997; Palsboll et al., 1997b). This difference may result from the way glaciations affect the large continuous feeding and breeding habitat of humpback whales, in coasts open to the ocean between the tropics and ice fronts, as contrasted to the more reduced and fragmented habitat of belugas and narwhals in circumpolar coasts and rivers.

Even if glaciations narrow the area of warm waters isolating the east North and South Pacific wintering grounds, the mechanism by which humpback whales from both hemispheres meet or disperse needs consideration. Acevedo & Smultea (1995) have found that humpback whales from the Northern and Southern Hemispheres currently overlap their winter distribution in Central America. Ladrón de Guevara-Porras (2001) observed that humpback whales in the Mexican Pacific have a higher relative abundance where and when sea surface temperature is close to 25°C. The spatial and seasonal distribution of this isotherm is variable as a result of the El Niño/La Niña oscillation. These findings suggest that, driven by climatic change, wintering humpback whales from both hemispheres may
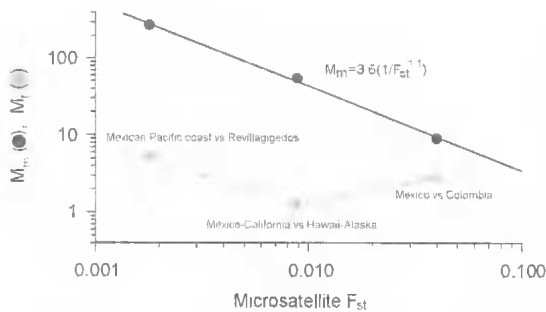
FIG. 4. Sex-biased dispersal of humpback whales at different population structure levels. Female gene flow (M_f) was estimated from the F_{st} for the mitochondrial control region. Male gene flow (M_m) was estimated substracting M_f from the total gene flow obtained with four microsatellite loci. The function fitted for male dispersal in dependence of population differentiation is shown ($r^2 > 0.99$). MtDNA data are from Baker & Medrano-González (in press) and nuclear genetic data are unpublished results from Baker & Vázquez-Cuevas.

enlarge their temporal and spatial distribution in the wintering grounds of the American Pacific. A critical overlap in the spatial and seasonal distribution of North and South Pacific humpback whales in their wintering grounds around Central America, may thus allow intermingling between these populations. Trans-oceanic nuclear gene flow by males can result from gametic exchange during an early or late winter wandering without dispersing permanently between oceans. Trans-equatorial mtDNA gene flow, however, requires that females themselves, not just their gametes, somehow shift their migratory cycle from the winter of one hemisphere to the other. Considering the seasonal feeding habits of humpback whales, such a migratory shift would require two consecutive winter seasons without a transit to the feeding grounds. Although presumably more difficult than the gametic exchange of nuclear genes, trans-equatorial dispersal and a shift in migratory cycles could be facilitated by the occurrence of highly productive areas close to or in the wintering grounds of the east Pacific such as the Sea of Cortés, the Dome of Costa Rica and other small areas in the coasts of México and Central America (Love, 1975; http://seawifs.gsfc.noaa.gov/SEAWIFS/IMAGES/CZCS.html). There is increasing evidence that humpback whales feed in winter grounds, especially in colder years when schooling fishes, such as sardines, may be abundant (Gendron & Urbán, 1993). Feeding in wintering grounds is a factor that may increase the spatial and temporal

overlap between North and South Pacific humpback whales favouring trans-oceanic gametic exchange by males. It is known also that a number of humpback whales, not yet demographically identified, spend the summer feeding in the Sea of Cortés (Urbán & Aguayo, 1987). Research on the identity, migration and ecology of mysticetes in the Sea of Cortés (e.g. Tershy et al., 1990), may enlighten such a process.

CONTEMPORARY CLIMATE EFFECTS. Although humpback whales appear to prefer a particular sea surface temperature, at a definite place and time their relative abundance can vary greatly without a defined pattern. Between years and regions, the temporal profiles of pod occurrence and relative abundance are different (Ladrón de Guevara-Porras, 2001) indicating the existence of complex social dynamics. For the 1998/99 winter in the Mexican Pacific, the temporal profiles of the different sex/reproductive status classes (Fig. 5) show a higher abundance of males which changes in parallel with the abundance of non-nursing females, though with a larger variation. Male abundance roughly varied inversely to fluctuations in nursing females except during the late breeding season. This suggests that movements of males in the Mexican Pacific wintering grounds follow the opportunity to find a receptive female and that, being more abundant in breeding grounds, the fluctuation of male abundance amplifies the smaller unpredictable variations of female abundance. Changes in local relative abundance are interpreted as dispersal to neighbouring breeding areas. In general, aggregation of humpback whales changes parallel to the global relative abundance. However, the temporal trajectories of abundance and aggregation follow a complex pattern similar to a strange attractor and which is a wide cycle with Socorro Island (Fig. 6; Appendix). Male abundance in the Mexican Pacific coast is lower and with smaller and more frequent variations compared to Socorro Island (Figs 5, 6). This may reflect the fact that the coastal breeding grounds are a large continuous area between Southern Baja California and the mainland coast which allow whales to move easily and spread all along the breeding ground. The Revillagigedo Islands, however, are small and relatively isolated. Whales here have a higher local relative abundance and move less frequently between islands making dispersal events more rare and abundance/aggregation fluctuations larger and less complex compared to the Mexican Pacific coast (Ladrón de Guevara-Porras, 2001).
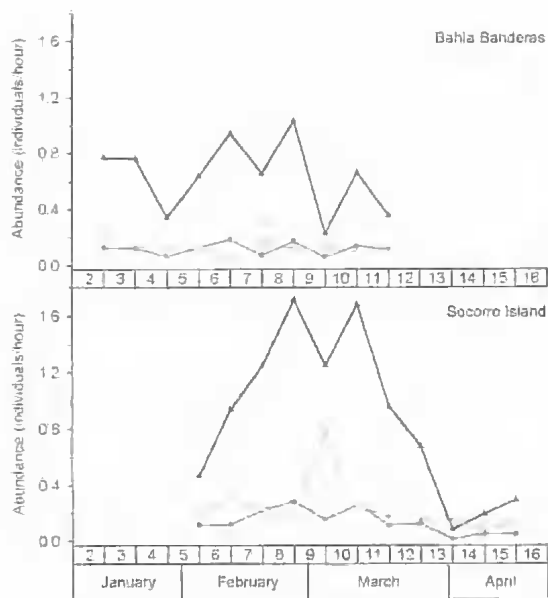
FIG. 5. Relative abundance profiles of males (tringles, black), non nursing females (circles, gray) and calving females (squares, light gray) during the 1999 winter in the Mexican Pacific mainland coast (Bahia Banderas) and the Revillagigedo Archipelago (Socorro Island). Numbered blocks show the weeks elapsed after January 1. The relative abundance of each sex/reproductive status class (f_{xr}) was calculated in weekly periods using equation (4). Boat-based observation effort was 234 hours for Bahia Banderas and 269 hours for Socorro Island.
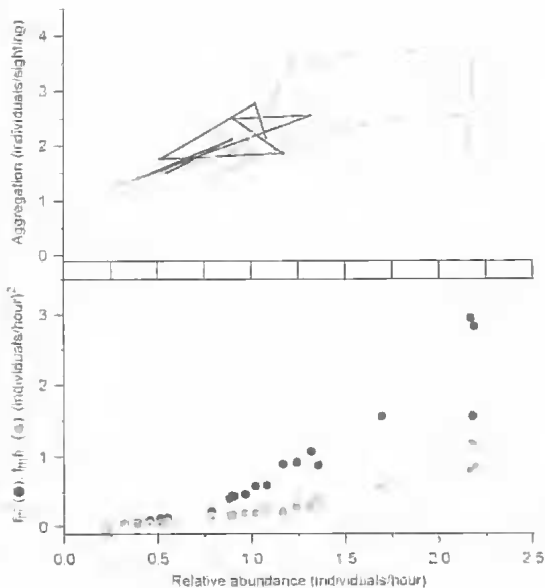

FIG. 6. Interactions among humpback whales, as functions of relative abundance, during the 1999 winter in the Mexican Pacific. Upper graph: Aggregation in Bahia Banderas (black) and Socorro Island (light gray). Lines show trajectories in time. Lower graph: Encounter rates among males (f_m^2, black) and between males and females ($f_m f_f$, light gray).

Because of its definition, the encounter rate between males and females increases proportionally with increase in total abundance. Encounters among males, however, vary at a higher rate indicating that local increments of abundance, despite favouring encounters between males and females, greatly increase the intensity of competition among males. The approach of such competition to a critical value may then promote dispersal events and thereby, sudden decreases of local abundance from which abundance/aggregation may rise again (Figs 5, 6). Thus, male competition for mating and dispersal in response to small unpredictable fluctuations in the local abundance of receptive females may drive male gene flow in the border of chaos and therefore generate, in the long term, its $1/f$-distribution at different population structure scales (Appendix).

DISCUSSION

Global climate change has the potential to affect all marine life through changes on prey availability, areas for breeding and even by the direct physical damage of ultraviolet radiation. Chittleborough (1991) has hypothesised that global warming may severely affect Southern Ocean ecology because of positive feedbacks between disturbances of physical and biological factors among which the CO_2 sink is critical. For humpback whales, the characteristic winter behavioural displays associated with pre-copulatory competition among males for a low number of receptive females in breeding grounds (Tyack & Whitehead, 1983; Baker & Herman, 1984; Whitehead, 1985; Brownell & Ralls, 1986; Brown et al., 1995; Clapham, 1996; Craig & Herman, 1997), the dependence of warm and coastal waters for reproduction (Dawbin, 1966; Ladrón de Guevara-Porras, 2001) and the association of population history to climate change (Medrano-González et al., 1995; Baker & Medrano-González, in press), may all derive from energetic constraints to female

reproduction. The basis of such restraints is not currently understood though they are known from the study of life history and reproduction and seem related to feeding ecology (Chittleborough, 1958, 1965; Clapham & Mayo, 1987a,b; Straley et al., 1994; Juárez-Salas, 2001). Given the sensitivity of humpback whale reproduction and dispersal to environment variation, climate change in this species may also have an impact through a reduction in periodic trans-oceanic gene flow. Already, severe El Niño events have resulted in large masses of warm water settling along the equatorial Pacific coast of the Americas (Enfield, 1989). Such water masses could obstruct the narrow corridor of gene flow between adjacent regions of both hemispheres, leading eventually to complete genetic isolation and even speciation between oceanic populations. This antitropical mode of population differentiation is actually involved in the speciation of many cetaceans and has been described by Davies (1963) long before genetic data were available. Therefore, in addition to the immediate effects of climate change on the abundance of baleen whale populations, our study on humpback whales raises concern about long-term alterations on the phylogeographic structure and thereby evolutionary potentialities of this and other species inhabiting the eastern tropical Pacific.

ACKNOWLEDGEMENTS

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APPENDIX

A BRIEF ON CHAOTIC DYNAMICAL SYSTEMS

It is traditionally believed that the complexity of a system's behaviour corresponds to the complexity of its structure and thus to the complexity of a scientific explanation for it. The analysis of complex behaviours is therefore often devoted to statistical dissections of multifactorial relationships and historical accounts of facts which are conceived as accidents as they are considered non repeatable and resulting by chance given a particular conditions set. Studying climate, Lorenz (1963) discovered that some simple systems may exhibit unpredictable behaviour which, however, is not random and which is now called chaos. Chaos appears in systems having at least a set of opposing processes which, in a critical state, yield a solution very sensitive to small variations. It may be guessed that many phenomena may involve transition to chaos. Indeed, chaos is ubiquitous and it is actually in the very origins of ordered phenomena as life.

Chaotic systems are self similar at different scales; this property is called fractality because the corresponding

geometric sets may have non-integer dimensions. The circulatory system, for example, is a branching set with topological dimension of 3 but is functionally a hybrid between volume and area with fractal dimension of 2.4. The chaotic dynamics underlying biological functions and its dimensional hybridism is the very basis for the pervasion of allometry in biology. Another property of chaotic systems is adaptation. Heart rate, for example, is chaotic and this allows the organism to adapt to a changing and unpredictable environment. Genetists know the importance of genetic diversity for the evolutionary adaptation of species being such a diversity a fractal branching set of cladogenetic processes. In general, organisms as replicative systems away from thermodynamic equilibrium live in the border of chaos and are adaptive.

A dynamic system is any whose behaviour changes in time. The examination of such systems includes the temporal profile of quantities which describe the system's behaviour and also the relationship between its independent variables. The plot of those variables is called phase-space. When the system has only one variable, the state at time t is related with the state at time $t+\tau$. In chaotic systems, trajectories in the phase-space are not predictable. Such trajectories, however, occupy a particular area of the space. The phase-space areas mostly visited by the system are called attractors. If trajectories in an attractor are complex, that is, not closed curves, the attractor is called strange. The distribution of fluctuations size is also of interest. The variation of the quantities used to describe the system is called noise. Thus, the distribution $1/f^\alpha$ is also called $1/f^\alpha$ noise where α is defined by the autocorrelation in the system motions. In a system like a roulette, there is no correlation between consecutive throws and in the long term all possible results will be equally frequent giving a flat distribution in which $\alpha\sim 0$. If the roulette results are colors, we may call its distribution as white noise. In a system like a particle in a gas, the position of the particle strongly correlates with its previous position and this correlation is rapidly loss in time. The distribution of motion sizes in a log-log plot is a steeply decaying line with $\alpha\sim -2$. The distribution of this Brownian motion is thus called brown noise. In a chaotic system, motions are partially correlated, they

are neither random nor deterministic and the size of fluctuations distributes with $\alpha\sim 1$. Pink noise is the term given to these phenomena.

For wintering humpback whales, we hypothesise that competition between males for a low number of receptive females makes them disperse between neighbouring areas (Fig. 5). Dispersion events may probably be in the border of chaos (Fig. 6) making gene flow of males self similar at different scales of population structure. Gene flow of females, instead, seems more subjected to historical contingencies dependent from environment changes (Fig. 4). Modelling of this requires refinement of what the facts are and consideration of a proper spatial structure. It is interesting that the size and continuity of wintering grounds, as contrasted by the Mexican Pacific coast and the Revillagigedo Islands, appear to have important implications in the dynamics of dispersal and thus on the phylogeographic structure of populations.

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